

# The ecology and growth patterns of *Cleistogenes* species in degraded grasslands of eastern Inner Mongolia, China

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## Summary

1. *Cleistogenes* is an important perennial grass genus found in the pastoral steppes of eastern Inner Mongolia. Despite its dominance in many grassland types, the value of *Cleistogenes* as a key genus for sustainable grassland development has only recently been recognized. To understand better how to manage *Cleistogenes*-dominant grasslands, an experiment was conducted in China, to characterize the growth patterns of two *Cleistogenes* species (*C. polyphylla* and *C. squarrosa*) in relation to environmental parameters.

2. Sampling exclosures were established on uniform grasslands at Mangha and Liuhe gachas. Over two growing seasons (1999–2000) vegetation cover, green and dry biomass by species, species height and tiller density of *Cleistogenes* were measured at about monthly intervals starting in mid-May and ending in mid-October. *Cleistogenes polyphylla* at Mangha and *C. squarrosa* at Liuhe accounted for > 50% of green biomass. Neither species made any significant growth before late June, even though soil moisture was available and a large number of tillers were present that had survived the subzero winter intact. In contrast, other species (*Prunus sibirica*, *Potentilla* spp. *Aneurolepidium chinense*) produced up to 500 kg ha<sup>-1</sup> biomass in early spring.

3. A relationship between temperature and green weight (wt) tiller<sup>-1</sup> indicated that *Cleistogenes* required an average air temperature > 20 °C to initiate growth, most probably due to its C4 photosynthetic pathway. In this region, temperatures above 20 °C also coincide with periods of most reliable rainfall, which may explain the success of *Cleistogenes* in grassland degraded by overgrazing. In contrast, competing C3 species (e.g. *Stipa* spp. and *Aneurolepidium chinense*) initiate growth earlier in spring when rainfall is highly variable and when small plants are most exposed to severe grazing pressure by livestock emerging from winter in poor condition.

4. Where *Cleistogenes* spp. completely dominated the grassland, the length of the growing season was shorter and feed shortages in early spring became more acute than for grasslands dominated by C3 species. Livestock producers can minimize this effect by adopting management tactics such as resting pastures in spring to maintain a balance between C3 and C4 perennial grasses. Further research is needed to establish when grazing and strategic rest have most impact on the stability of *Cleistogenes*-dominant grasslands.

*Key-words:* C4 photosynthetic pathway, grassland steppe, rest management, temperature response

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## Introduction

*Cleistogenes* is a perennial grass genus that is endemic to the steppes of northern China. Grasses of the genus

were originally described in the 1930s when they were classified variously as *Diplachne*, *Cleistogenes* and *Kengia* (Packer 1960). The taxonomy of the group was revised in 1983 with the publication of a key that included 10 identified species (Ma, Fu & Chen 1983). Compared with species found in the world's high latitude grasslands, *Cleistogenes* is most similar to blue grama *Bouteloua gracilis* Steud., a short bunch grass found in the mixed grass prairies of North America

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(Gu 1993). Both genera have the C4 photosynthetic pathway (Redmann, Yin & Wang 1995; Fair, Lauenroth & Coffin 1999), are well adapted to grazing and are usually found in low altitude areas.

In a study of the grassland resources in Xilin Gol League in Inner Mongolia, Poissonet & Li (1990) reported that *Cleistogenes* spp. were frequently the dominant or key species, with *Carex duriuscula* C.A. Mey and *Artemisia frigida* Willd. dominant in low altitude steppe. In the same region, Liu (1963) reported that *Cleistogenes squarrosa* (Trin.) Keng was only a minor component of grasslands dominated by *Stipa baicalensis* Roshev. and *Filifolium sibiricum* (L.) Kitamura, and only slightly more frequent where *Stipa grandis* P. Smirnov was dominant. However, in the eastern confine of the *Stipa*–*Aneurolepidium* steppe subcoregion, *Cleistogenes* spp. often became codominants with *Aneurolepidium chinense* (Trin.) Kitagawa and *Artemisia frigida*, especially under moderate to heavy grazing (Li 1989). Due to its grazing tolerance, *Cleistogenes* is a key indicator where overgrazing is the prime cause for convergence of different grassland communities (Li 1989). Wang (1992) defined the relationship between *Cleistogenes* abundance and grazing pressure in a study of *Stipa baicalensis* steppe in which *Cleistogenes squarrosa* became dominant at 55% utilization, but declined when grazing utilization was increased above 70%.

Despite its dominance in many of the grassland types in eastern Inner Mongolia, the value of *Cleistogenes* as livestock forage and a key species for the sustainability of these important grasslands has not been widely recognized. However, in Xingan League, where large pastoral areas are heavily grazed, *Cleistogenes* is the most important perennial grass in both meadow and sandy grasslands. In a survey of Front and Middle Banner undertaken in 1997, *Cleistogenes* accounted for 10–50% of cover in all the grassland sites surveyed, excluding wetlands (Treskonova, Michalk & Tong 1999). In many cases *Cleistogenes* was the dominant grass that was selectively grazed by sheep and goats in preference to *Stipa* (*baicalensis* and *grandis*), *Aneurolepidium chinense* and *Arundinella hirta* Tanaka. These findings are contrary to those of Jiang (1990), who ranked *Cleistogenes squarrosa* behind *Aneurolepidium chinense* and *Stipa grandis* in importance both as livestock forage and for stabilizing degraded steppe grassland.

At least three of the 10 *Cleistogenes* species described by Ma, Fu & Chen (1983) are found in Xingan League. These include *C. polyphylla* P.C. Keng, *C. caespitosa* Keng and *C. squarrosa*. *Cleistogenes polyphylla* usually occurs as part of the *Stipa baicalensis* steppe type along with *Arundinella hirta*, *Filifolium sibiricum*, *Aneurolepidium chinense*, *Lespedeza* spp., *Potentilla* spp. and *Festuca ovina* L., whereas *Cleistogenes squarrosa* is found as part of the *Stipa grandis* steppe along with *Koeleria cristata* Bertol., *Agropyron cristatum* (L.) Gaertn., *Artemisia* spp. and *Potentilla* spp. (Li *et al.* 1980). Li *et al.* (1980) showed that these associations

reflect climatic adaptation, with *C. polyphylla* preferring wetter, cooler areas and *C. squarrosa* preferring warmer areas. The climatic preference of *Cleistogenes caespitosa* is uncertain, but analyses of the 1997 survey suggest that it is similar to *C. polyphylla* but only in very heavily grazed areas (D.L. Michalk, unpublished data).

We propose that *Cleistogenes* remains active and productive in degraded grasslands (Wang 1992) because of its C4 photosynthetic pathway. Such plants require a higher temperature to activate growth than C3 plants. This means that *Cleistogenes* growth signals coincide with a more reliable rainfall period (late May–early June) than its C3 competitors (e.g. *Stipa* spp., *Aneurolepidium chinense*). It does not waste scarce root reserves trying to initiate growth earlier in the season when rainfall is erratic and grazing intensity is most intense. In contrast, *Stipa* spp. respond at lower temperatures and commence growth on stored root reserves a month earlier than C4 plants. However, if water stress stops active growth, or severe grazing occurs before root reserves are replenished, *Stipa* is weakened, resulting in a reduction in basal diameter or even death.

This pattern of compositional change from C3 to C4 grasses is commonly observed in temperate grasslands (Gu 1993). Reports on the C3 to C4 transition are often expressed as a change from perennial to annual grasses, such as that described by White, Campbell & Kemp (1997) for improved perennial ryegrass *Lolium perenne* L. pastures in New Zealand. The consequence of invasion by C4 annuals is a loss in community stability because these annual species only occupy space and utilize resources when moisture is available. However, the C3 to C4 transition in Chinese grasslands is more likely to occur as a two-part process: first, there is a change from a C3 perennial grass to *Cleistogenes* spp., and only when additional intense stress is placed on the ecosystem do C4 annual grasses invade the gaps created in the grassland. An important consequence of the first stage of transition for livestock production is a possible change in seasonal distribution of forage. Because C4 perennial grasses commence growth later in spring relative to C3 perennials, and often mature earlier (Bai & Xu 1994), the dominance of C4 grasses often represents a significant loss in forage production. This has serious implications for livestock production in Inner Mongolia, as a period of severe feed shortage frequently coincides with peak demands by lactating animals in early spring.

To understand better the role of *Cleistogenes* species in livestock production and restoration of degraded steppe grassland, a study was conducted in Xingan League in 1999–2000 to characterize the growth patterns of *Cleistogenes* spp. in relation to environmental parameters and other grassland components. This information was then used to recommend management action to maintain stable and sustainable grasslands for livestock production.

## Materials and methods

### EXPERIMENTAL SITES

The study was conducted in Front Banner of Xingan League, China, at demonstration exclosures established in Mangha (122°04' E; 46°01' N) and Liuhe (122°16' E; 46°13' N) gachas in 1998. Mangha gacha is located in Charsen sumu on medium-condition meadow grassland that is typical of the *Stipa baicalensis*–*Filifolium sibiricum* association and now dominated by *C. polyphylla*. Originally the experimental exclosure had a *Prunus sibirica* L. shrub layer, but at the time the research was undertaken shrub density was low due to a history of heavy grazing prior to fencing the exclosure in April 1998. The area chosen for this part of the study had not been grazed for a 12-month period prior to commencing the experiment in May 1999.

A second study area was established at a similar exclosure located at Liuhe gacha in Ergutu sumu on poor-condition meadow grassland that was a degraded form of the Mangha grassland. Historically subjected to intense use by livestock, overgrazing had reduced sward diversity and led to dominance by perennial grasses (mainly *C. squarrosa*) with C4 annual grasses [namely *Chloris virgata* Sw., *Setaria viridis* (L.) Beauv. and *Eragrostis pilosa* (L.) Beauv.] and *Artemisia frigida* colonizing gaps created in the community by grazing. Like Mangha, the Liuhe exclosure was not grazed for a 12-month period prior to the commencement of the experiment in 1999.

The soils of both sites are classified as 'chestnut' in the regional survey for Xingan League but are mapped as castanozems by Shi, Cai & Gao (1990). These relatively light-textured soils are classified as silty sands or silts with < 20% clay. Using standard tests 20 random cores (0–10 cm) were collected at each site, from which subsamples were analysed to describe the chemical attributes of the soil at each site. The results showed the following differences: Mangha was more acidic [ $\text{pH}_{(\text{water})} = 6.9$ ] and had a much lower cation exchange capacity (CEC) of 23.8 me 100 g soil<sup>-1</sup>, whereas Liuhe was more alkaline [ $\text{pH}_{(\text{water})} = 8.7$ ] with a higher CEC (62.6 me 100 g soil<sup>-1</sup>) but a lower level of available potassium (Mangha 186 mg kg<sup>-1</sup> vs. Liuhe 91 mg kg<sup>-1</sup>). There was no difference in the available nitrogen (195 mg kg<sup>-1</sup>), available phosphorus (4 mg kg<sup>-1</sup>) and organic matter (2.9%) status of the soils between sites.

The temperate, semi-arid and continental climate at the experimental exclosures is influenced by the south-east monsoon (Shi, Cai & Gao 1990), with two-thirds of the precipitation falling in the June–August period (Table 2). There is little rain or snow in winter. Highly variable April–June rainfall (coefficients of variation 106%, 68% and 64%, respectively) results in unreliable early spring forage production in most years, and September rainfall is too late to produce significant plant growth because it coincides with falling temperatures, when there is a high probability of damaging frosts. Mid-winter temperatures plummet to < -25 °C, which freezes the soil to a depth of 2 m (Li, Xia & Chen 1990). The combined effect of temperature and rainfall means that potential production is not as high as expected from the average rainfall (472 mm) over the 6-month growing season (May–September).

### EXPERIMENTAL DESIGN, MEASUREMENTS AND STATISTICAL ANALYSIS

The experiment was laid out at each grassland exclosure in a randomized block design with the six sampling times (Table 1) replicated five times. The replications were located on a diagonal in a relatively uniform patch of grassland at each exclosure. Within each replication, seven quadrats (each 0.1 m<sup>2</sup> in size) were selected and identified with permanent pegs in May 1999 and a new group laid out in May 2000. Random numbers were used to allocate the six sampling dates (Table 1) to the quadrats with one plot left as a spare. Vegetation parameters measured at each sampling date prior to harvesting the biomass included: total plant cover estimated visually; *Cleistogenes* density by counting the number of tillers per quadrat; and natural height of *Cleistogenes* plants measured in centimetres with a ruler.

After these measurements were taken, the plots were harvested with hand shears to a height of 1 cm. The collected material was first sorted into *Cleistogenes* and 'other' species and then further subdivided into green and dry material. Each sample was weighed and dried in a microwave oven for 2–6 min (depending on sample volume), as recommended by Jones & Griffith (1968). Checks were made at about 1-min intervals to ensure that over-drying did not occur. Material was reweighed following drying to determine dry matter content of *Cleistogenes* and other species. Regrowth was measured

**Table 1.** Sampling dates for the Mangha and Liuhe sites

Experimental site1	Sampling dates					
	1	2	3	4	5	6
Mangha 1999	16 May	11 Jun	23 Jul	11 Aug	6 Sep	20 Oct
2000	23 May	16 Jun	7 Jul	17 Aug	27 Sep	26 Oct
Liuhe 1999	23 May	13 Jun	14 Jul	11 Aug	7 Sep	20 Oct
2000	25 May	15 Jun	6 Jul	17 Aug	20 Sep	27 Oct

**Table 2.** Rainfall and average temperature for Front Banner, 1998–2000

Climatic parameter	Months												Total
	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	
<b>Rainfall (mm)</b>													
Mean*	1.0	2.4	5.0	16.3	32.1	90.3	166.6	97.5	40.4	15.4	3.6	1.6	472.2
1998	1.0	3.6	7.3	16.3	40.2	74.8	285.6	311.9	56.0	19.4	7.6	0.2	823.9
1999	1.1	2.0	13.4	4.7	13.8	62.9	69.1	56.4	18.4	41.8	4.4	1.3	289.3
2000	8.3	0.6	0.7	45.3	8.6	34.0	85.0	92.4	9.2	15.1	5.2	7.7	312.1
<b>Mean temperature (°C)</b>													
Mean*	-14.0	-9.5	-2.4	7.6	15.1	20.6	22.9	17.6	10.5	1.7	-4.0	-11.1	
1998	-16.1	-6.7	0.5	11.1	17.6	19.2	22.8	17.7	12.3	0.9	-8.6	-10.2	
1999	-12.4	-7.2	-7.6	8.2	14.6	20.6	25.3	18.4	10.5	1.8	-2.6	-10.4	
2000	-17.2	-10.1	-1.6	7.0	17.0	20.9	23.4	22.1	17.5	5.5	-7.9	-17.0	

\*Mean monthly rainfall (mm) and average temperature (°C) calculated for the period 1980–99 for Front banner, Inner Mongolian Autonomous Region.

in August (May cut only) and September (June through August plots) using the same harvesting procedures. Rainfall and temperatures for the experimental period were obtained from Xingan Animal Husbandry Bureau for Front Banner (Table 2).

The data for each parameter were analysed using Genstat software (Payne 1988) as an analysis of variance of the effect of cutting time split in space (grassland type at each enclosure) and time (years), using a method described by Steel & Torrie (1960). The analysis enabled the effects of grassland type, year and sampling time within year to be examined along with the interactions between these main effects. Least significant differences based on error terms from the appropriate stratum of the analysis of variance for measured parameters were used to differentiate between significant and non-significant means.

## Results

### CLIMATE DATA

Climatic conditions in 1998 were the wettest recorded over the last 20 years, whereas 1999 and 2000 were dry, receiving < 66% of the long-term average. Such years occur with a frequency of about 1 year in 4 (Table 2 and Fig. 3). Drought months defined as receiving < 50% of the long-term average occurred in April, May, July and September in 1999, and May, June, July and September in 2000 (Table 2).

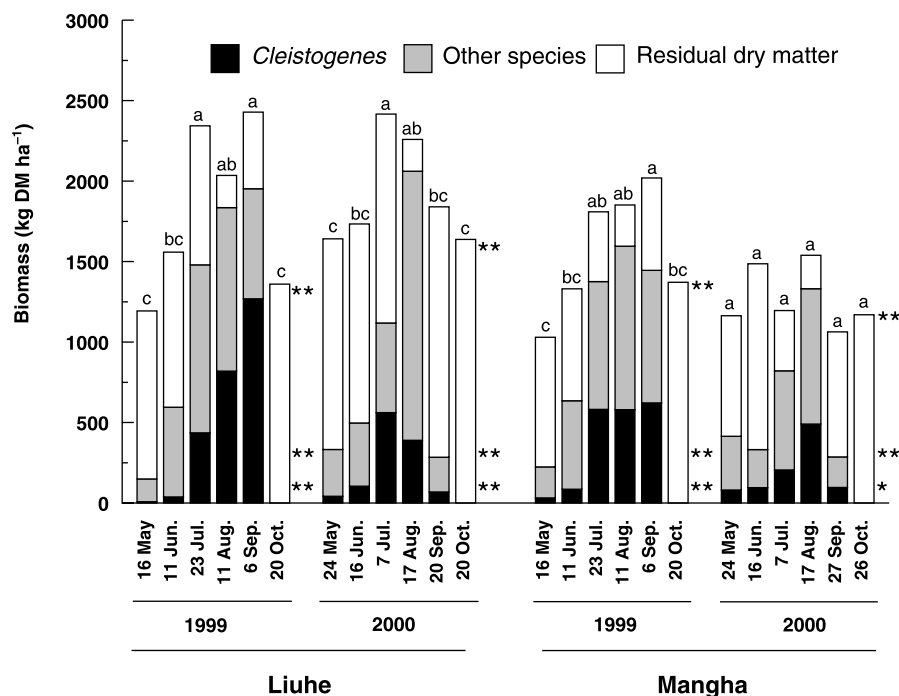
### SEASONAL PRODUCTION

Overall, the Liuhe grassland type was more productive ( $P < 0.01$ ), producing 30% more biomass than Mangha (mean 1871 vs. 1420 kg ha<sup>-1</sup>). More important, peak production of green dry matter was 35% to 55% higher ( $P < 0.05$ ) at Liuhe than Mangha in September 1999 and August 2000, respectively (Fig. 1). In 1999 this was due to significantly higher *Cleistogenes* production ( $P < 0.05$ ) that occurred between mid-August

and early September (Fig. 1) following mid-summer rain (Table 2). However, in 2000 the difference was due to other perennial grasses (e.g. *Aneurolepidium chinense*) that increased at Liuhe in the absence of livestock grazing, with a reduction in *Cleistogenes* (Table 3).

At both enclosures, *Cleistogenes* made no significant new growth before late June/early July (Fig. 1), irrespective of the incident rainfall. For example, *Cleistogenes* did not respond significantly to the abnormally high rainfall received in April 2000 (Fig. 1 and Table 2). This was not caused by a low presence of *Cleistogenes* in the grassland sward before late June because large numbers of carry-over tillers were still present at both grassland enclosures (Table 4), indicating that there was an abundance of *Cleistogenes* plants that survived the winter intact (two-thirds of dry standing residual in May and June). Rather, the rapid growth made by *Cleistogenes* later in the growing season relative to the other species present appeared to be related to the temperature response of this C4 grass (Figs 2 and 3).

There were also significant differences ( $P < 0.01$ ) recorded in the contribution of 'other' species to green dry matter biomass measured at each enclosure (Fig. 1), and in the composition of this group (Table 3). In 1999 at Liuhe, there was a large proportion of other perennial grasses such as *Aneurolepidium chinense* (23% of green biomass) and *Arundinella hirta* (7%), and a much smaller contribution from forbs such as *Potentilla* spp. that made up 10% of total plant biomass. Due to the absence of grazing, the taller growing *Aneurolepidium chinense* out-competed *C. squarrosa* in 2000 and limited any invasion of the prostrate forbs (Table 3). In contrast, at Mangha in 1999 forbs (e.g. *Leontopodium* sp. and *Filifolium sibiricum*) accounted for more than 85% of the 'other' green dry biomass, as there were few perennial grasses other than *Cleistogenes* present in the ungrazed enclosure (Table 3). In 2000 a shift in forb composition was noted, with a significant increase ( $P < 0.05$ ) in the proportion of *Potentilla* spp. and *Prunus sibirica* present at Mangha at the expense of *Leontopodium* sp. The increase in *Prunus* shrubs was



**Fig. 1.** Total production (kg ha<sup>-1</sup>) and the contribution of *Cleistogenes* and other species to total green matter (dry matter; DM) measured at Mangha and Liuhe, 1999–2000. The same letter at the top of histograms indicates that there was no significant difference in total yield between sampling dates within years and grassland types at  $P < 0.05$ ; \* and \*\* indicate significant differences at  $P < 0.05$  and  $P < 0.01$  between sampling dates within years and grassland type within pasture components; NS indicates no significant difference.

**Table 3.** Botanical composition (percentage of green biomass) of pastures at Liuhe and Mangha exclosures measured in August 1999 and 2000

Species	Liuhe exclosure		Mangha exclosure	
	11 Aug 1999	17 Aug 2000	11 Aug 1999	17 Aug 2000
<i>Cleistogenes</i> spp.	44	19**	36	37
<i>Aneurolepidium chinense</i>	23	47**	0	0
Other perennial grass	7	9	1	1
Legume	3	5	3	3
Sedge	13	9	4	6
<i>Potentilla</i> sp.	4	6	6	18**
<i>Leontopodium</i> sp.	3	0	31	17**
<i>Filifolium sibiricum</i>	0	0	12	9
Other forbs	3	5	4	2
<i>Prunus sibirica</i>	0	0	5	12*
Total green biomass (kg ha <sup>-1</sup> )†	1836	2062	1596	1332

\* and \*\* indicate significant differences at  $P < 0.05$  and  $P < 0.01$  between years within grassland types (sites).

†Total green biomass reported in Fig. 1.

due to the combined effect of wet conditions in 1998 (Table 2) and exclusion from livestock grazing, whereas the increase in *Potentilla* spp. was a result of high April rainfall in 2000 that enabled *Potentilla* to invade the sward that had significantly ( $P < 0.05$ ) less vegetative cover than the Liuhe grassland (17% vs. 38%).

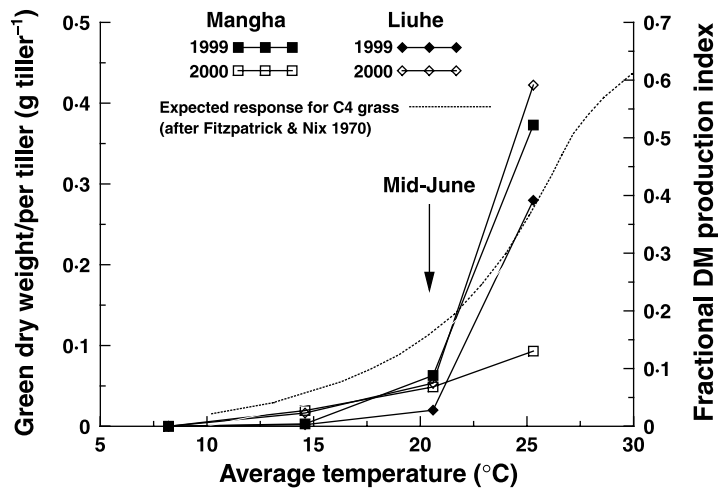
average monthly air temperature (°C) for Front Banner against the mean green weight per tiller derived from the production (Fig. 1) and tiller density data (Table 4). The effect was further examined using daily average temperature (data only available for 1999) and production of *Cleistogenes* and ‘other’ species (Fig. 3).

Both data sets indicated that *Cleistogenes* tillers required the average air temperature to exceed 20 °C for a period of several days to stimulate growth. Exponential fits for the relationship between average monthly temperature and tiller green dry weight

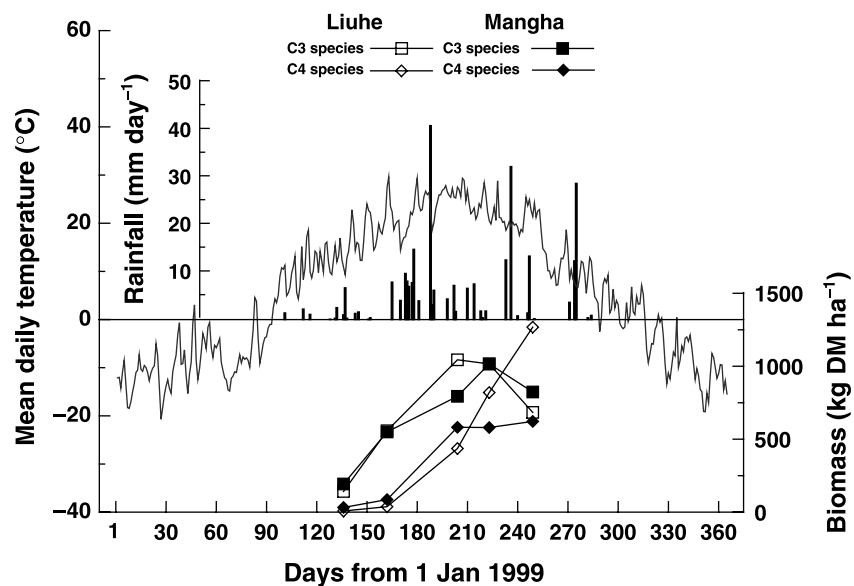
**Table 4.** Density (number m<sup>-2</sup>) of *Cleistogenes* tillers in May–October

Site location/year	<i>Cleistogenes</i> tiller density (number m <sup>-2</sup> )									
	May	Jun	Jul	Aug	Sep	Oct	May recut†	Jun recut†	Jul recut†	Aug recut†
Mangha 1999	215abc	156cd	158cd	212abc	174bcd	164bcd	250a	232ab	148cd	104d
2000	296a	144bc	158bc	160bc	120bc	90c	178b	144bc	120bc	–
Liuhe 1999	268a	204abc	152cd	248ab	180bcd	108d	220abc	180bcd	130d	108d
2000	270a	190bc	140cd	144cd	112d	89d	216ab	140cd	118d	96d
NS	NS	NS	*	NS	*	NS	*	NS	NS	

†Tiller density from recut plots was measured in September and significant differences due to cutting were determined by comparing recut means with the September-only cut tiller density. Means within sites and years followed by the same letter are not significantly different at  $P < 0.05$ . \* Indicates significant differences between exclosures and year means within cutting times at  $P < 0.05$  (l.s.d.<sub>(5%)</sub> = 70 plants m<sup>-2</sup>). NS indicates no significant difference.



**Fig. 2.** Relationship between average monthly temperature (°C) and growth of *Cleistogenes*, 1999–2000.



**Fig. 3.** Relationship between average daily temperature (°C), daily rainfall (mm) and growth of *Cleistogenes* for 1999.

explained > 95% of the yield variability. This pattern was evident in both years (Fig. 2) even though the spring rainfall patterns were quite different (Table 2). This response was similar to the generalized temperature–dry matter production curve reported by Fitzpatrick &

Nix (1970) for C4 grasses (Fig. 2). In contrast, the ‘other’ component comprised mostly C3 grasses (*Stipa* spp. and *Aneurolepidium chinense*) and forbs (*Prunus sibirica*, *Potentilla* sp. and *Leontopodium* sp.) and commenced active growth at 10 °C (Fig. 3).

Once the temperature threshold for *Cleistogenes* growth initiation was reached, rainfall was sufficient (and by inference available soil moisture) to support rapid subsequent growth rates and tiller production of *Cleistogenes* spp. (Fig. 3). In general, *C. polyphylla*, the dominant species at the Mangha enclosure, produced twice as much green production per tiller in June as *C. squarrosa*, the dominant species at Liuhe (0.07 vs. 0.37 g tiller<sup>-1</sup>). This was a function of leaf size, with the larger leaf of *C. polyphylla* equating to 2–3 of the smaller leaves of *C. squarrosa*. However, *C. squarrosa* has the capacity to produce significantly more leaves per tiller than *C. polyphylla* and by August–September, green biomass per tiller was twice that of the less leafy *C. polyphylla* (0.43 vs. 0.23 g tiller<sup>-1</sup>) at equivalent tiller density (Table 4).

#### CLEISTOGENES TILLER PRODUCTION

The cyclic nature of tiller density is shown in Table 4. While *Cleistogenes* tillers remained intact over the winter period, not all the carry-over tillers present in May survived. A significant reduction ( $P < 0.05$ ) in tiller number (up to 45%) was observed over the May–July period at both sites in both years (Table 4). During the main growing season for *Cleistogenes*, when moisture was available, density increased due to a flush of new tillers, and in 1999 densities at both enclosures had reached pre-growth levels in August. However, although August rainfall in 2000 was higher than in 1999, it occurred in only one rainfall event that did not initiate new tiller development in 2000 (Table 4). A second cycle of tiller mortality was observed from September onwards so that post-growth tiller density was 77% and < 40% of the August peak for Mangha and Liuhe, respectively. Individual tillers were not tagged, but one could speculate that losses measured after August comprised mostly tillers that had lasted through the previous winter and were decomposing at a rapid rate under the high moisture and temperature conditions. Supporting evidence for this speculation was that no corresponding decline in green *Cleistogenes*

production was measured over this period of tiller loss in 1999 (Fig. 1) when rainfall occurred in several storms. The subsequent fate of new tillers formed in 1999 was not recorded as new sampling plots were selected for 2000 to avoid the carry-over effects of cutting on plant responses.

Defoliation had a differential effect on tiller density, depending on time of cutting, enclosure and year. For example, defoliation in May and June in 1999 stimulated tillering and significantly increased tiller number relative to the September density by 44% and 33% at Mangha ( $P < 0.05$ ), but decreased tiller density by 15% and 40% when cut in July and August (Table 4). In 2000, there was no significant effect of cutting on tiller density, although a similar trend was evident for the May cut. At Liuhe, defoliation in May also increased tiller density but this was significant ( $P < 0.05$ ) in 2000 only (Table 4). These responses to defoliation over time indicate that there is little difference in tiller production between *C. polyphylla* (dominant at Mangha) and *C. squarrosa* (dominant at Liuhe). There was no significant difference in plant height (Fig. 4) or height to the first green leaf (ranging from > 1 cm in May to about 4 cm in September; data not presented) between *Cleistogenes* species.

Defoliation at different times had a significant but variable effect of *Cleistogenes* at Liuhe in both years ( $P < 0.05$ ), but little effect at Mangha (Fig. 5). For example, in July 1999 defoliation had a critical effect on *C. squarrosa* production at Liuhe that resulted in the lowest total green biomass yield of all the multiple-cut treatments, while a delay in defoliation until early September maximized green *Cleistogenes* production (Fig. 5). In contrast, no cutting regime changed green matter production of *C. polyphylla* at Mangha in 1999. These results suggest that July rather than early spring is a critical period to rest the pasture in order to maintain or to increase the contribution of *C. squarrosa* in meadow grasslands, but that the timing of rest is less critical for *C. polyphylla*. Results in 2000 were more variable due to low rainfall in May and June (Table 2).

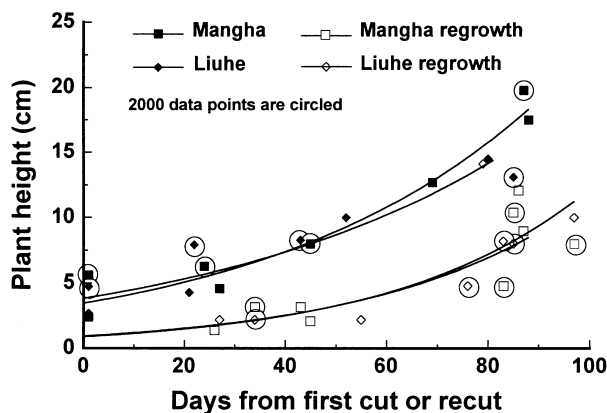
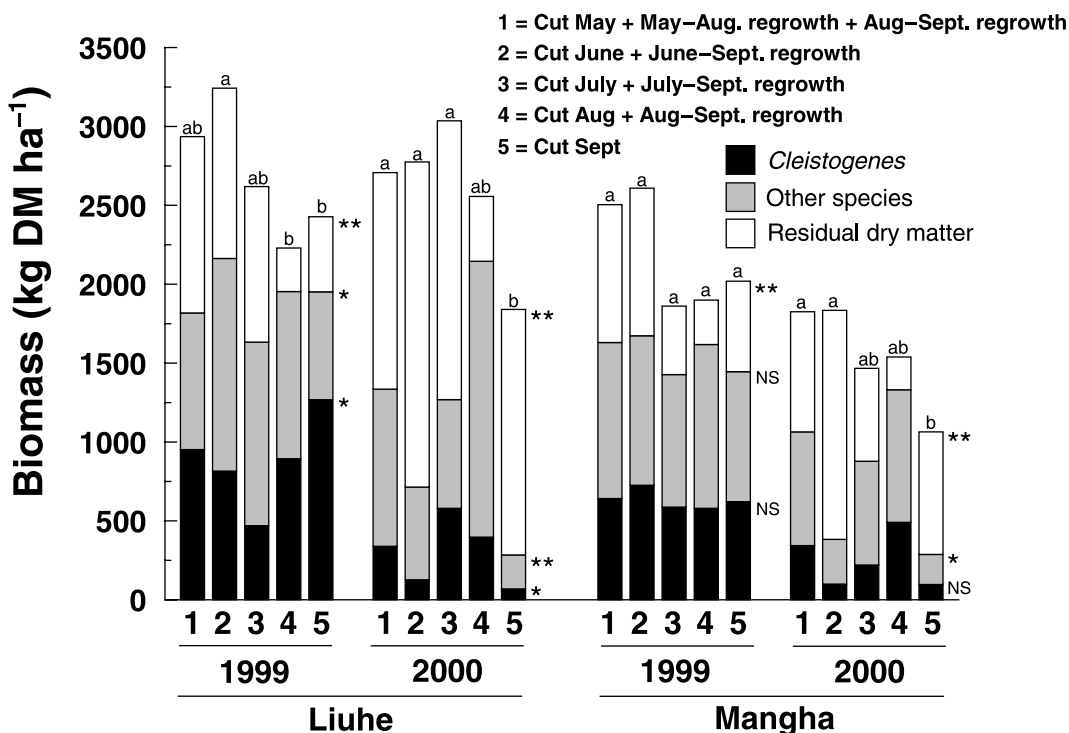


Fig. 4. Mean height (cm) of *Cleistogenes* spp. measured at Mangha and Liuhe between mid-May and early September, 1999 and 2000.



**Fig. 5.** Effect of multiple cutting on green biomass production at Mangha and Liuhe in 1999 and 2000. The same letter at the top of histograms indicates that there was no significant difference in total yield between sampling dates within years and grassland types at  $P < 0.05$ ; \* and \*\* indicate significant differences at  $P < 0.05$  and  $P < 0.01$  between sampling dates within years and grassland type within pasture components; NS indicates no significant difference.

#### RESIDUAL DRY MATTER

There was a significant amount of residual dry matter present at the start of the experiment ( $806 \text{ kg ha}^{-1}$  at Mangha and  $1044 \text{ kg ha}^{-1}$  at Liuhe). This was expected because both study areas had been excluded from grazing since May 1998. Despite the large initial difference in residual dry matter between exclosures, by August the levels were similar (Fig. 1). This represented disappearance rates of about 68% and 84% for Mangha and Liuhe, respectively. However, residual biomass did not decompose at a constant rate, but disappeared differentially with time (Fig. 1). This was related to rainfall and temperature, with little decomposition occurring in early spring when temperature was low (Table 2). Only when temperature increased to  $17^\circ\text{C}$  or more did rapid decomposition occur. This was most noticeable at Liuhe where  $> 600 \text{ kg ha}^{-1}$  of residual biomass was lost in a month.

Standing residual biomass started to accumulate from early September onwards, and by mid-October all above-ground forage was mature and desiccated by subzero temperatures. Over winter, only 55% of residual dry matter was still standing intact at Mangha, compared with 80% at Liuhe (Fig. 5). This was due to the difference in grassland composition, with *C. squarrosa*, *Arundinella hirta* and *Aneurolepidium chinense* (the latter two included in the 'other' species component) remaining standing whereas the forbs that dominated the 'other' species component at Mangha collapsed after frosting.

In spring 2000, a large increase in standing residual biomass (53%) was measured at Mangha. This was due to good rainfall that initiated growth of C3 forbs followed by a protracted dry period that burnt off the new season growth, which was subsequently deposited as litter on the soil surface. This did not occur at Liuhe because of a lower proportion of forbs and the drought hardness of the C3 grasses (e.g. *Aneurolepidium chinense*).

#### Discussion

Information on the seasonal distribution of grassland production and biomass composition is necessary to formulate carrying capacities and develop appropriate management practices. The relationship between grassland production and abiotic factors has been an important theme of grassland research in Inner Mongolia, and a number of studies (Bai & Xu 1994; Bai, Xu & Li 1994; Chen *et al.* 1994; Lu 1994; Xiao *et al.* 1996) have shown a significant relationship between seasonal rainfall and biomass. Correlations tend to be quite specific with a significant linear relationship, with May and August rainfall accounting for most of the year-to-year variation in biomass. However, few of these studies have examined the impact of temperature on the composition of the biomass produced.

The aim of this current study was to describe the contribution to seasonal production of *Cleistogenes* spp., the perennial grass that is dominant in the typical meadow grassland of Xingan League. While it has been commonly noted that all the known *Cleistogenes*



species increase under moderate to heavy grazing (Li 1989; Wang 1992), the authors know of no studies that have examined the relationship of *Cleistogenes* to climatic cues. Previous studies undertaken in Xingan League (Treskonova, Michalk & Tong 1999) suggested that temperature, not moisture, was the prime factor that determined the seasonal production pattern and explained the survival of *Cleistogenes* in most of the grasslands in Front and Middle Banners.

As a C4 plant, *Cleistogenes* requires higher temperatures to activate tillers and initiate new season growth (Redmann, Yin & Wang 1995). Poor early spring production is a phenomenon common to meadow and sandy grasslands in Xingan League. In such grasslands, *Cleistogenes* spp. may account for more than half the biomass produced, as was the case in this experiment, and in highly degraded grasslands *Cleistogenes* spp. may be the only perennial grasses present. These facts highlight the timeliness of gaining a better understanding of the ecology of *Cleistogenes* spp. so that systems can be developed to manage this genus effectively as an integral part of the grasslands in Xingan League.

The most important new information to emerge from the present study is the strong relationship between temperature and the growth of *Cleistogenes* (Fig. 2). Neither *C. polyphylla* nor *C. squarrosa* made any significant growth until average air temperature exceeded 20 °C. At the same time a range of other C3 species (e.g. *Prunus sibirica*, *Leontopodium* sp., *Aneurolepidium chinense* and *Artemisia frigida*) were able to initiate growth prior to mid-June (Fig. 3), suggesting that moisture was not limiting.

For livestock production this means that where *Cleistogenes* spp. completely dominate the grassland, the length of the growing season is effectively shortened and feed shortages in early spring will become more acute than for grasslands dominated by C3 species. In the current study, a range of other grasses and forbs (depending on site) were able to take advantage of early spring rain and provide > 500 kg ha<sup>-1</sup> of production before *Cleistogenes* spp. commenced growth (Fig. 1). This highlights the merit of management practices that maintain a balance of C3 and C4 perennial grasses in the same grassland swards. At Liuhe, spring rest (April to early June) proved to be an effective means of enhancing the contribution of *Aneurolepidium chinense* in poor-condition meadow grassland dominated by *C. squarrosa*. From a practical viewpoint, management should aim to maintain *Cleistogenes* spp. cover within a range of about 35–50%. Above this level, *Cleistogenes* spp. may prove to be too competitive, preventing other species from contributing to early season production.

Further information on the population demography of *Cleistogenes* species is needed. For example, it is not known how long *Cleistogenes* plants live nor how frequently new individuals are added to the population. Does *Cleistogenes* rely on seedling recruitment to maintain population size or is vegetative spread by fragmentation the most important recruitment

mechanism? Fair, Lauenroth & Coffin (1999) reported that the ability of blue grama *Bouteloua gracilis*, the C4 American bunchgrass equivalent to *Cleistogenes*, to produce long-lived genets allowed it to maintain its population in the community because occupation of resource space for long periods prevented recruitment of other species.

A similar mechanism may apply to *Cleistogenes* spp., as few seedlings have been observed in our extensive studies of two different grassland ecosystems in Xingan League between 1997 and 2000. However, tiller densities of *Cleistogenes* spp. similar to those reported for Mangha and Liuhe (i.e. 150–300 m<sup>-2</sup>) have been measured in situations ranging from heavily grazed communal grassland to managed exclosures. Despite these high densities, there are still large gaps in resource space of the grassland communities, irrespective of condition class, providing opportunities for invasion by either *Cleistogenes* spp. or other species. The fact that this does not occur in situations where *Cleistogenes* is the dominant species suggests that resource gaps below-ground are more important than bare spaces between plants at the soil surface in determining community change. This is logical as soil water is the factor most likely to control plant growth and community structure in these short-grass steppes (Lauenroth, Dodd & Sims 1978).

A large extensive root system is essential to monopolize soil water. Little is known about the root system of *Cleistogenes* spp., although it is generally acknowledged that the root biomass in *Aneurolepidium chinense* and *Stipa grandis* grasslands is several times larger than the above-ground biomass (Chen & Hwang 1988). Our field evidence suggests that *Cleistogenes* spp. have superior capacity to prevent invasion even by aggressive C4 annual grasses when moderately grazed. It has also been noted that moderate to heavy grazing significantly reduces root biomass (Guodong & Zhijun 1993). In turn, this weakens a plant's capacity to control the soil water regime. From Wang's (1992) data, utilization of total biomass within the 55–70% range is likely to reduce competitiveness of *Cleistogenes* spp. through reductions in both root biomass and tiller density.

While these negative effects of grazing on ecosystem stability and health need to be minimized by implementing appropriate management strategies such as tactical rest and stocking rate reductions, grazing can also have beneficial effects on grassland productivity. Results in Table 4 showed that *C. polyphylla* production at the Mangha exclosure increased when cut twice rather than once early in the same season. However, defoliation at any time at the Liuhe exclosure had a consistent negative effect on new tiller formation of *C. squarrosa*. This implies that the same management strategies applied to grasslands dominated by different *Cleistogenes* species may produce different results.

Currently, livestock overgraze these grasslands. Continuation of utilization at the current level will lead to a progressive decline to the point where *Cleistogenes*

spp. will be placed at risk. While reduction in grazing pressure is an obvious remedy, this is rarely successful or sustainable unless accompanied by other management tactics that provide the producer with appropriate tools to actively manage the grassland system. Active management for these *Cleistogenes*-dominant grasslands may well focus on ensuring that residual biomass levels are adequate to maintain tiller populations at healthy levels, protect the soil surface against erosion and provide a steady flow of litter back to the soil (Guo & Zhu 1989) to maintain nutrient flows (Zhang *et al.* 1990). In addition, the concern that biomass production is concentrated over a shorter period as the proportion of *Cleistogenes* spp. increases under high utilization provides the incentive for livestock producers to consider using pasture rest tactics to maintain a balance between C3 and C4 plants.

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